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LEAF SPOTS OF THE ELM

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(WITH PLATES VIII–X AND ONE FIGURE)

Introduction

About eighteen species of the genus *Ulmus* are known (2), widely distributed throughout the cold and temperate regions of the Northern Hemisphere. Six of these species, *U. americana*, *U. fulva*, *U. racemosa*, *U. alata*, *U. serotina*, and *U. crassifolia*, are native to America and occur naturally from Labrador to southern Mexico. None, however, occur west of the Rocky Mountains. *U. alata*, *U. crassifolia*, and *U. serotina* are tender and do not grow well in the northern states, but are quite extensively used for lawn and avenue trees in the south. *U. americana*, the most widely distributed American species, occurs in practically every state east of the Rocky Mountains, and in Canada. It is the most characteristic tree of the northeastern states, and is very widely used for street planting and as an ornamental tree for lawns.

Among the fungous enemies of the elm are a number of forms which cause leaf spots, the most important of which will be discussed in this paper. Ordinarily none of these diseases is of much importance economically, but in severe cases they may injure the tree materially by causing premature defoliation. This saps the vigor of the tree, and if the severe attack is repeated during a number of consecutive seasons, may even result in its death, or at

least may weaken it to such an extent that it is not able to withstand the adverse factors in its environment. In a nursery of young elm trees these leaf spots may do much more damage than when they occur on older trees.

Most important American leaf spot

Distribution and history

Chief among the fungi causing leaf spots of the elm in this country is *Gnomonia ulmea* (Schw.) Thüm. This disease, known as the elm leaf spot or elm leaf scab, occurs most commonly on

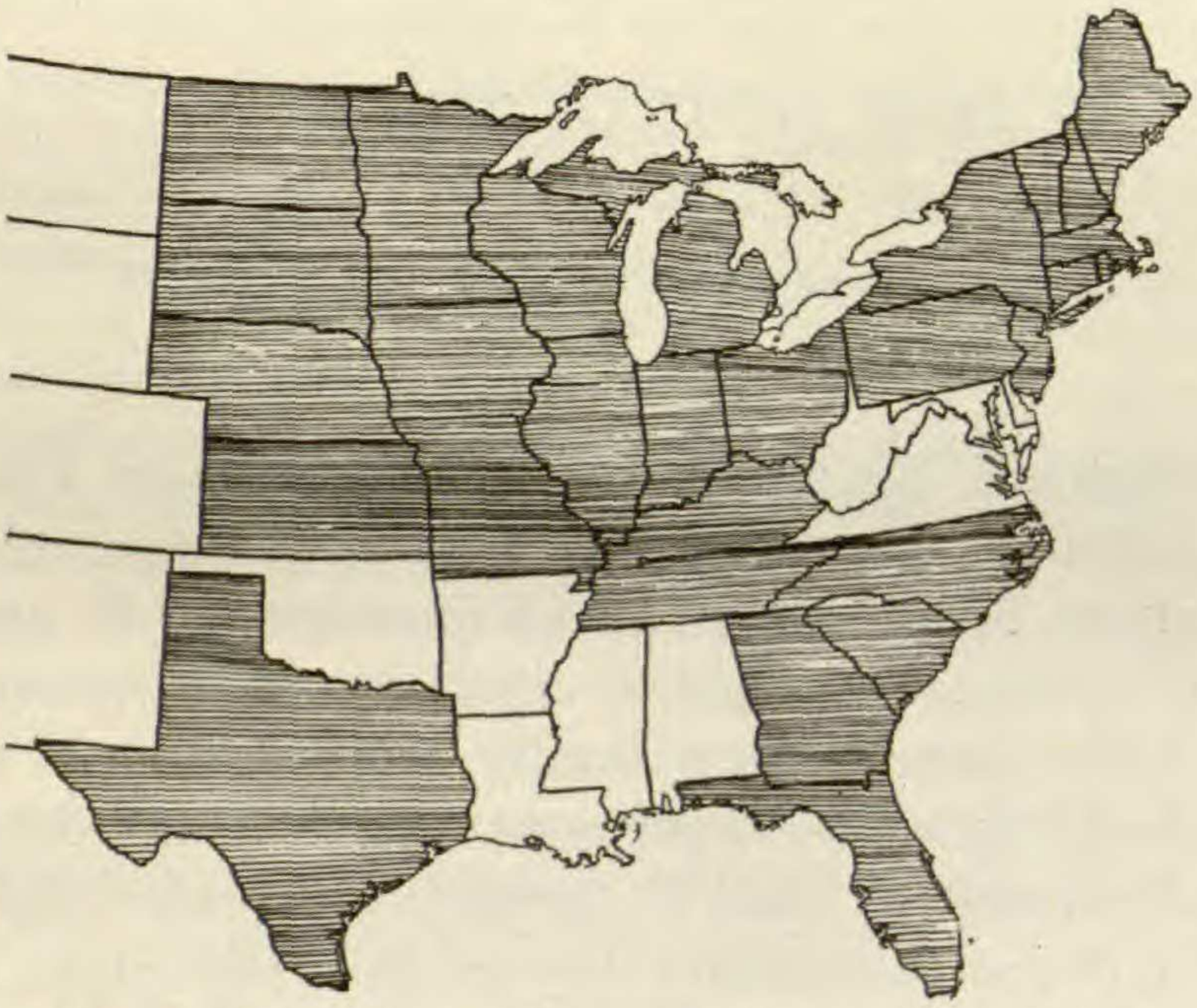

Fig. 1.—Distribution of *Gnomonia ulmea* in United States

U. americana, and is found in greater or less degree throughout the entire range of its host. The writer has examined exsiccati specimens of it which were collected in New York, Massachusetts, Vermont, Maine, New Hampshire, Rhode Island, Connecticut, Pennsylvania, Ohio, Michigan, Indiana, Illinois, Wisconsin, North Dakota, Iowa, Nebraska, South Dakota, Missouri, Kentucky, Tennessee, North Carolina, Georgia, South Carolina, and Texas, as well as several from Canada. Text fig. 1 gives a better idea of its wide distribution than does this list of states. It is more than probable that it occurs also in the remainder of the states east of

the Rocky Mountains, but has not been reported. In addition to the normal host, *U. americana*, specimens have been examined on *U. fulva*, *U. alata*, *U. crassifolia*, and *U. racemosa*, and it is quite probable that it may occur also on *U. serotina*, the only other American species. It has not been seen on any European or other foreign elm, however, collected either in this country or abroad, nor is there any account in literature of its occurrence on such. It may be concluded, therefore, that this fungus is strictly an American species.

The fungus was first described by SCHWEINITZ (34) as *Xyloma ulmeum*, in 1818, on leaves collected at Aiken, South Carolina. His material was immature, and consequently his description was incomplete and inadequate. Fig. 7 is a leaf from the type collection from which his description was taken. This specimen is one of SCHWEINITZ' exsiccati in the Museum of the Academy of Natural Sciences at Philadelphia. Comparison of this figure with figs. 3–5, showing infected leaves collected by the writer, indicates that the fungus with which SCHWEINITZ worked and the one discussed in the early part of this paper are identical.

A few years after SCHWEINITZ' original description, FRIES (19) described a disease of the American elm as caused by *Sphaeria ulmea* Fr., but gave *Xyloma ulmeum* Schw. as a synonym, showing that he had seen SCHWEINITZ' previous description and recognized that he was dealing with the same organism. His description added but little to the earlier one of SCHWEINITZ. The next change in the taxonomic position of the fungus was made in 1878 by VON THÜMEN (39) when he placed it in the genus *Gnomonia* without explanatory comment or additional description. In his *Sylloge Fungorum* SACCARDO seems to have accepted this change with some reservations, since he placed the fungus in the section Dubiae of the Sphaeriales, under the name *Gnomonia ulmea* (Schw.) Thüm., without, however, explaining his reasons for doing so.

In 1892 ELLIS and EVERHART (16) made a further change in the name and taxonomic position of the fungus, apparently without being acquainted with the previous work of VON THÜMEN, since they made no mention either of his name or of *Gnomonia* in

their account of the synonymy of the organism. They called it *Dothidella ulmea* (Schw.) E. and E., thereby placing it among the Dothidiales, although they acknowledge that it is "anomalous on account of its ascigerous cells assuming the characters of perithecia." In 1915 THIESSEN and SYDOW (38), in a monograph of the Dothidiales, excluded it from that group and referred it back again to *Gnomonia* in the Sphaeriales, where it had previously been placed by VON THÜMEN. In addition to these various names, the fungus has been much confused by American plant pathologists and mycologists with an organism causing a leaf spot of European elms in Europe, *Systremma Ulmi* (Schleich.) Thiess. and Syd. (38), to which it has a superficial resemblance, and it has often been collected and reported under one or another of various lists of synonyms pertaining to that fungus.

In 1901 and 1902 STONE and SMITH (37) from Massachusetts reported attempts at controlling the disease by spraying with Bordeaux mixture, referring to the fungus as *Dothidea Ulmi* (Duv.) Wint., a synonym of *Systremma Ulmi*, in the first paper, and as *Dothidella ulmea*, a synonym of *Gnomonia ulmea*, in the second, although they made no reference to the discrepancy. In 1910 GÜSSOW (21) reported it from Canada as extending back upon the petioles of young shoots to their tips, which twisted downward and finally died. He stated that in no case did the young shoots so infected recover. In this same year CLINTON (8) from Connecticut reported that by July or earlier some trees had shed almost all their leaves. He stated that these trees later put forth a new crop of foliage which was entirely free from the disease, but that the other trees, not so severely infected in the beginning, showed all their leaves more or less affected, and shed them continuously throughout the season. He stated that when defoliation was most severe the young branches of the season also had fallen off. This latter observation confirms that made by Güssow in Canada. The writer has seldom seen so severe an infection as either of these, although in some localities the disease is severe enough each year to cause an incessant dropping of leaves throughout the summer and fall, which is a far from desirable characteristic in a lawn and avenue tree like *U. americana*.

Symptoms

The disease makes its appearance early in the spring, the amount of primary infection apparently being dependent to a considerable degree on the weather conditions, as it is much worse on the same tree in some years than in others. Clinton expressed the opinion that the only infection which occurred was the primary spring infection, and that there was no further spread during the summer. The fact that no conidial or summer stage had ever been found connected with the disease, and also his observation of trees which shed all their leaves early in the season and which later produced a new crop of foliage entirely free from spots, would tend to support this conclusion. The absence of the disease on the new crop of leaves, however, might have been due to weather conditions which were not favorable to the spread of the organism at that time. In any case, the writer has found a conidial stage constantly associated with the disease in every specimen examined, and the connection between the two stages will be clearly shown later. Observations show also that the primary infection is confined almost exclusively to the lowest leaves, and that it is much more abundant on the young seedlings, whose leaves are naturally closer to the ground, and to the ascospores which are the source of this early infection. Moreover, it is only on these young seedlings that twig and petiole infection has been observed, although there it is often quite severe, killing off the entire new growth.

The first evidence of the disease is a small whitish or yellowish fleck or blotch on the upper side of the leaf shortly after it has unfolded. This spot increases in size, and soon a number of small black specks begin to appear within the whitened area. As these enlarge they sometimes coalesce to form a single, coal black, stroma-like, subcuticular structure which is quite irregular in outline and varies from 0.5 to 2 or 3 mm. in diameter. As a rule, however, the individual stromata remain separate, when they appear to be somewhat concentrically arranged, forming a distinct spot, in most cases surrounded by a narrow band of whitish dead tissue as shown in fig. 12. Occasionally the black stroma, or the group of separate stromata, so closely grouped together as to seem to the naked eye to be a single one, may cover the entire discolored

area, without a border of whitish or lighter colored dead tissue. In this case it appears almost like a tar spot on the normal green leaf tissue, and reminds one of some of the species of *Rhytisma*. Later in the season the cuticle which covers the stroma wears away and gives the spot an ashen appearance, which is most pronounced near the edge. These black spots may be so numerous as to practically cover the entire upper surface of the leaf.

In addition to these black stromata, and much more prominent in the early stages of infection, although the reverse is the case later in the season, are the pustules of the conidial stage. They are quite abundant and conspicuous in the early spring, and it is hard to understand how they can have been overlooked for so long a time. They are subcuticular, irregular in outline, and dark, owing to the cuticle which is stained by the fungus, and which splits irregularly to allow the dispersal of the spores, which are extruded in small white masses. The pustules formed earliest seem to have but little or no stromatic base, although those formed later in the summer are almost invariably situated on a distinct stroma, which they may or may not entirely cover. This conidial stage will be discussed more in detail later.

Development of stromata

Beneath each one of the small, black, subcuticular stromata, as represented in fig. 13, early in its development, beginning about the latter part of May, there commences the development of the young perithecium of the causative fungus. The stroma now becomes somewhat looser in structure near its central region, beneath which the perithecium is to be formed. The normal cells of which the stromatic hyphae are made up are short, approximately isodiametrical (fig. 16), and contain comparatively little protoplasm, which little soon disappears, except in the basal layer of cells, and in those which are actively engaged in extending the edges of the stroma. They are more or less olivaceous to dilute brown in color, the depth of the hue depending on the age of the cell, but the very dark appearance of the stroma is due principally to a dark coloring matter which is not present in the cell wall to any extent, but seems to be excreted by the cells of the fungus

and deposited between their walls. A similar excretion of coloring matter was noted by KLEBAHN (22) in working with *Gnomonia veneta* (Sacc. and Speg.) Kleb. Within the looser portion of the stroma are to be found in this stage of its development other hyphae, which are very thin-walled, entirely filled with a very dense protoplasm, and have comparatively few septa. They stain pink or red with Pianeze IIIb stain (41), as do the other hyphae which enter into the formation of the young perithecium, but much more intensely. The ordinary stromatic elements, which have become comparatively inactive, take a green color with this stain. These deeply staining active hyphae ramify through the lower, looser portion of the stroma, a number of them turning upward near the center and breaking through to the outside, extending above the leaf surface as shown in fig. 16.

ASCOGONIUM

Immediately beneath this portion of the stroma there grows downward into the leaf tissue, between the epidermal cells and between the cells of the upper palisade tier (usually to a point near the lower edge of that layer), one of these hyphae which has become slightly larger in diameter. For convenience this hypha may be termed an "infection thread" or "suspensor," since it is the first of the fungal hyphae to invade the tissue of the host beneath the epidermal layer, and since in the early stages of its development the young perithecium gives the appearance of being suspended from the subcuticular stroma above by means of it. This hypha is accompanied in its growth downward into the host tissue by a number of other hyphae, consisting of short isodiametrical cells, which arise from the basal layers of the stroma and contain comparatively little protoplasm. They form a sheath for the broader, more deeply staining hypha, which for convenience only has been designated as an infection thread or suspensor. After growing to a point about midway down in the palisade layer, this cuts off a number of cells at its extreme end (fig. 16), usually three or four, which coil somewhat in the form of a spiral. Each one of these cells contains two or more nuclei, while the cells of the hyphae which constitute the sheath are uninucleate. These hyphae

meanwhile have continued their growth, dividing in such a manner as to produce a larger number of chains of cells which arrange themselves spirally about the central coil and form what is to become the wall of the perithecium.

This coiled structure is the ascogonium or "Woronin's hypha," described by various workers in a considerable number of Ascomycetes. I do not consider the hypha connecting it with the stroma above in any way analogous to a trichogyne, however, but rather as being similar to and corresponding to the hypha described by Miss DAWSON (14) as leading from the stroma beneath and giving rise to "Woronin's hypha" in *Poronia punctata*. The apparent differences between the two cases are that in *Poronia* the perithecium is formed in the upper part of the stroma, and the hypha which gives rise to the ascogonial coil comes up from below and does not leave the stroma; while in *Gnomonia ulmea* the perithecium is formed beneath the stroma in the tissue of the host, which renders it necessary for the thread which is to give rise to the ascogonium to leave the stroma and grow downward into the leaf tissue. In each case the hypha enters the perithecial primordium at a point which is finally located in the basal portion of the mature perithecium. In *Poronia*, however, after coiling to form the ascogonium, it continues to grow on beyond the perithecium to the outer surface of the stroma as a somewhat narrower thread, which reminds one of the trichogyne of *Collema*, as described by BACHMAN (3), of *Physcia* by DARBISHIRE (11), and of *Polystigma* by FRANK (18) and FISCH (17), but not by BLACKMAN and WELLSFORD (4). This "trichogyne" was not present in *Gnomonia ulmea*.

BROOKS (6), in working with *Gnomonia erythrostroma* (Auers.) Kleb., found an ascogonium similar to the one described for *G. ulmea*, and also certain structures which he called trichogynes. He was able to trace a connection between these hyphae and the peripheral layers of the young perithecium only, never with the ascogonium itself. These peripheral layers would correspond in fig. 16 to the sheathing hyphae *a*. Since more than one trichogyne passed through a single stoma in the case in which he was working, BROOKS concluded that more than one series of trichogynes was

connected with a single ascogonial coil. In *G. ulmea* also, as previously stated, one finds (fig. 16) certain hyphae which pass out through the upper leaf surface in a quite similar manner, although not through a stoma in this case, since stomata are absent on the upper surface of an elm leaf. In this case, however, there is no possibility of their being mistaken for anything else than vegetative hyphae. It is quite likely that those of *G. erythrostroma* are of a similar nature. BLACKMAN and WELLSFORD described in *Polystigma rubrum* trichogynes similar to those of BROOKS, but on account of an inability to trace a direct connection with the ascogonium, concluded that they were merely vegetative. In earlier papers FISCH (17) and FRANK (18) had both described and figured such connections and had designated the hyphae as true trichogynes. Although BROOKS continued to call the projecting hyphae in *G. erythrostroma* trichogynes, and although he found both ascogonia and spermatia present, he concluded that the trichogynes were no longer functional, and that fertilization did not actually occur through their agency. He suggested as a present function for them that they might serve as respiratory channels for the fungal hyphae within the leaf, where the assimilatory processes must necessarily have been considerably curtailed by the dying of the tissue. Such a function would also give reason for the existence of similar hyphae in *G. ulmea*, especially since the presence of the black stroma would tend even more to impair the respiratory processes in the host tissue beneath it.

The ascogonium in the young perithecium of *G. ulmea* soon begins to break up into segments, each cell becoming separated from the others. BROWN (7) noticed a similar segmentation of the ascogonium of *Xylaria tentaculata*, as did also Miss DAWSON in *Poronia*. They found that those segments gave rise to the ascogenous hyphae in the fungi with which they were working, but I have been unable to ascertain this fact with certainty in *G. ulmea* with the material at hand. It is almost a certainty, however, that this is the case here also, since the segments of the ascogonial coil can be distinguished near the base of the perithecium until after the asci have commenced their development.

FURTHER DEVELOPMENT OF PERITHECIUM

In the further development of the young perithecium all sign of the connection with the subcutaneous stroma soon disappears, as is shown in fig. 2, which is a slightly older stage. The structure has increased in size, chiefly by the enlargement of the portion which is later to become the perithecial cavity, but which is now filled with a dense pseudoparenchyma. The wall has also increased somewhat in thickness by the formation of new layers on the inside. As yet there is no sign of a beak or ostiole, although the wall cells on the lower side of the perithecium, opposite the stroma, are somewhat denser in protoplasmic contents, as is shown by the slightly darker color. Fig. 8 shows a still later stage of development in which the perithecium has practically doubled in size, since the two figures are of the same degree of enlargement. The central area has enlarged and the wall become still thicker. The darkly stained portion is composed of young asci which are not yet clearly differentiated. On account of the nature of the material, the leaves showing this stage of development having first been collected and dried and later softened with lactophenol, as well as on account of the very small size of the nuclei, the cytological and other minute details of this development could not be accurately determined. The main portion of the perithecial cavity is entirely filled with a very fine pseudoparenchymatous material, which when crushed or teased out appears merely granular in structure, with some slight evidence of anastomosing hyphae. In the original description of the fungus, SCHWEINITZ mentions the granular nature of the perithecial contents. The beak or rostrum and the ostiole are here seen in the earliest stages of their development. The same group of more deeply staining wall cells, mentioned in connection with fig. 2, is still evident, but has increased in size to form a sort of plug of tissue, which by its growth forces the outer layers of the perithecial wall outward and downward on the lower side to form the outer wall of the beak. As the multiplication of these actively dividing cells continues, their long axis changes from horizontal, as at first, to a direction parallel to that in which the beak is being developed. The cells nearest the center of this elongating beak separate in their continued growth, leaving a

channel throughout its entire length which becomes the ostiole. This channel is lined with periphyses or hairlike structures which are hyphal outgrowths of the inner or lining layer of cells. These periphyses all point in a direction outward from the perithecial cavity, and so form a one-way passage from the spore bearing portion to the outside of the leaf. As the development of the beak nears completion, each layer of cells, whose increase has brought about its elongation, produces at its lower end one or more of these periphyses to each cell, so that the lower end or outer opening of the ostiole is surrounded by a considerable brush of them. These later stages of the development of the ostiole are seen in fig. 1, which shows two perithecia in an almost mature condition. The beaks are slightly longer than normal at this stage of maturity, but in all other respects the perithecia are typical. No further elongation of the beaks occurs until the ascospores are fully mature and ready to be discharged, sometime in the early spring, at which time they again begin growth and continue until they have just broken through the lower epidermis. In this stage, which is the condition in which they pass the winter, the lower end of the beak is still within the leaf tissue and merely pushes out the lower epidermis in the form of a hump or tubercle. In the spring, when they have just broken through, these beaks, although short, are quite conspicuous on account of their fresh dark brown or almost black color.

The asci in the figure last referred to are not yet mature, and it will be seen that the pseudoparenchyma is still present. This tissue is composed of small hyaline cells, filled with a very dense granular protoplasm, and with very thin walls; in fact, the walls are little more than membranes. It occupies the entire central region before the development of the asci, which grow out into it, and apparently it is used up by the asci in their growth, as no crowding of the tissue is apparent ahead of them. Such an interascicular pseudoparenchyma has been described by STEVENS (35), who used it as the basis for the formation of a new genus, *Desmotascus*. He considered it an instance of delayed dissolution of the pseudoparenchymatous central region of the developing perithecium to form the central cavity, and suggested that, since this

structure was not clearly seen without good thin microtome sections, the same thing may exist in other perithecia and have been overlooked because the microtome was not used. The finding of such a structure in *Gnomonia ulmea* would tend to support such a hypothesis. REDDICK (29), working with *Guignardia bidwellii*, found that when the first asci were developing not nearly all the pseudoparenchyma was gone, and that, when crowded together by the growth and expansion of two asci, it gave the impression that paraphyses were present. He also expressed the opinion that these cells were absorbed by the growing asci. This case differs from that found in *Gnomonia ulmea* and also from that described by STEVENS in *Desmotascus* only in that the pseudoparenchymatous cells in the latter two fungi never appear to be crowded by the invasion of the asci.

The asci originate from the basal portion of the perithecial cavity, and also from the sides to a point about halfway to the top. The perithecial walls are composed of from 10 to 12 rows of cells (fig. 1), the outer one or two layers of which have assumed a bright golden brown color. It is at about the time when the ostiole is being developed that this coloration of the wall begins. Until that time the wall has been entirely hyaline. From this time on, as the perithecia age, this color becomes constantly darker, until about midwinter, when it is almost black. The outer surface of the perithecium is smooth, and there are no loose hyphae connecting it with the leaf tissue in which it is borne.

When mature the perithecia are nearly spherical or usually somewhat wider than deep. They vary considerably in size, but average about 250–300 μ in diameter and 150–200 μ in depth. The ostiole is usually about 100 μ long and 75 μ wide, but may reach a considerably greater length. The size of the perithecium is so great that the upper epidermis is elevated in the form of small tubercles, and the beaks push out the lower epidermis in the same manner, before they break through it. They do not extend any distance beyond the outer surface of the lower epidermis, as do so many of the species of *Gnomonia*, but merely reach through it. When the over-wintered leaves have been soaked in water, the perithecia may be picked out with the point of a sharp scalpel, and

on account of the absence of any hyphae connecting them with the leaf tissue, they leave a smooth cavity or locule in the leaf.

Asci and ascospores

In mature perithecia the asci are very much confused in their arrangement, owing to the fact that the older ones are broken loose from their attachment and pushed toward the top of the perithecial cavity by the younger ones. There are no paraphyses. The asci are oblong-cylindrical or somewhat club-shaped in form, and have a short stalk at the base which may be either straight or bent toward one side. The wall is hyaline, thin below, but thickened in the upper half (fig. 19), and does not color with iodine. At the upper end of the ascus is a pore surrounded by a ring of thickened tissue which is strongly refractive toward light. In optical section as seen from the side this ring presents the appearance of two small spheres arranged side by side in the apex of the ascus. The asci measure 45–55×9–11 μ. The spores are very characteristic also. They are hyaline, elongate-elliptical, or obovate-oblong, and have a septum near the lower end, thus becoming unequally two-celled. They are eight in number, sub-biseriate, and measure 8–10×3–3.5 μ. The small cell at the lower end of the spore averages about 2 μ both in length and breadth. There is a slight constriction at the septum. Some epiplasm is present in the mature ascus along with the spores.

Expulsion and germination of ascospores

As previously stated, the asci in a mature perithecium become loosened from their attachment at the base and crowded toward the apex of the perithecial cavity in a somewhat disordered mass. In the process of expulsion of ascospores an entire ascus enters the lower part of the ostiole and is held in place by the periphyses until the pressure produced by the absorption of water, which must be present to allow the ascospores to be discharged, becomes sufficient to bring about the discharge of the spores. These pass outward through the periphysis-lined ostiolar channel to the surface of the ostiole, where they are expelled with some force, and under natural conditions are evidently dispersed by currents of air. Early in March leaves were found which had passed the

winter in the open under natural conditions, on which occurred perithecia in such a stage of development as to expel ascospores within two days after being brought into the laboratory. It was found that spore expulsion was very slow and limited or did not occur at all when the leaves were kept too moist or when maintained in a saturated atmosphere, such as occurs when they are placed on moistened filter or blotting paper in a closed Petri dish. When the lid of the dish is removed, however, and the leaves are alternately allowed to become dry and again moistened by adding water to the filter paper beneath them, the spores are expelled in considerable quantities. If they are then caught on a glass slide, either dry or coated with a thin film of egg albumin, glycerine, or some such adhesive, it is found that the spores are deposited in clusters or groups of eight. Later, as a very large number of spores are discharged from a single ostiole, this grouping of course is not apparent. The best method for catching the expelled spores was that used by ANDERSON and RANKIN (1) in working with *Endothia parasitica*, as described previously. The glass slide was suspended by means of match sticks fastened to it near the ends, thus bringing it 3 or 4 mm. above the opening of the ostiole.

KLEBAHN (**27**) has shown that this method of spore expulsion is general to *Gnomonia* and to many other fungi which have *Gnomonia*-like, beaked ostioles. The expulsion of the asci into the neck of the ostiole appears largely due to the swelling pressure of the ascus. When dry, the ascus with its contained spores occupies considerably smaller space than after it has been moistened with water. Many workers have maintained that ascospores are ordinarily liberated one at a time, and such may be the case here, since I have been unable to observe the actual act of expulsion of the spores from the ascus, but the clusters of the spores intercepted on a glass slide suspended above the opening of the ostiole are always in groups of eight, and give the impression of having been expelled in a group, as was found by ANDERSON and RANKIN to occur in *Endothia parasitica*.

Many attempts have been made to germinate the ascospores of *Gnomonia ulmea* under various conditions, and on a number of different nutrient media, ranging from distilled water, tap water,

extract of dried elm leaves, and sugar solutions, to solid media such as the agars of cornmeal, bean, potato, Brazil nut, onion, elm leaf, and plain washed agar. In distilled or tap water the spores swelled considerably, especially the larger cell, and sometimes a spore would give the appearance of being on the point of sending out a germ tube from the side of the larger cell, but this never occurred. This is in accordance with the results obtained by KLEBAHN (**27**) in *Gnomonia alniella* and *Gnomoniella tubiformis*, which he was not able to grow in culture, but is contrary to his results with *Gnomonia platani* and *G. leptostyla*, both of which grew well on nutrient media, the latter even producing the perithecial stage in such cultures. It would seem that the ascospores of *Gnomonia ulmea*, as in *G. alniella* and *Gnomoniella tubiformis*, require the stimulation given by the green leaf of the host plant itself in order to induce germination. WOLF (**42**) found that this was the case in *Diplocarpon rosae*, the ascospores of which would not even germinate in a drop of water in which a portion of a green leaf of the host had been placed, but must be placed in a drop of water directly on the living leaf itself. This assumption was later confirmed by experimentation. Toward the middle of March a number of twigs were cut from an elm and placed in the greenhouse with their cut ends immersed in water. In about three weeks the buds on these twigs unfolded. A number of the young leaves were removed and placed in a moist chamber with their surfaces in contact with a slide on which a large number of the expelled spores of *Gnomonia ulmea* had been intercepted as previously described. Intimate contact was secured by moistening the surface of the slide to which the spores adhered with a drop of water. By removing the leaf it was possible to examine the spores on the slide by means of a microscope, but never was one of them found to have germinated. Later, when the leaves on the trees outside the greenhouse had begun to unfold, the same experiment was attempted again, and in twelve hours it was found that a considerable number of the spores in contact with the leaves had germinated. This led to an examination of the tree from which the leaves used in the first experiment had been obtained, and it was ascertained to be an English elm, *Ulmus campestris*.

This led to a further attempt to germinate the spores on the leaves of both the English and the Scotch elm, *U. glabra*, but without success in either case. A considerable percentage of germination, however, was always obtained with *U. americana*. These experiments would seem to indicate that the germination of the ascospores of *Gnomonia ulmea* is dependent on a special stimulus of some sort exerted by the leaves of susceptible species of *Ulmus*, but which is absent in the leaves of other species of the same genus, just as it is absent in tap or distilled water, and the various liquid and solid nutrient media in which attempts were made to grow the fungus.

At the end of twelve hours of contact with the leaf of the American elm under suitable moisture conditions, as previously stated, the spores were found in various stages of germination. Wherever two spores lay in contact with each other and also with the leaf, there was noted a brown coloring matter deposited between them. This coloring matter is similar to that previously mentioned as being deposited between the hyphae of the stroma and on the lower side of the cuticle. The germ tube usually arises from the large cell of the spore only, as shown by fig. 20, although in a very few instances the small cell also may send out one. Germination apparently can occur from any point in the spore, although usually the germ tube makes its exit from the side of the large cell. One can tell where the germ tube is going to form even before any swelling occurs by the excretion of the brown coloring matter on the outside of the spore wall at that point. As the tube grows, the coloring substance is deposited along its entire length, except at the extreme apex, but in considerably greater density at the point where it leaves the spore. The substance is present in greater abundance also wherever two germ tubes touch or cross each other.

INOCULATION WITH ASCOSPORES

On April 6 a number of abscissed twigs of *Ulmus campestris*, whose leaves had unfolded in the greenhouse, were inoculated with the ascopores of *Gnomonia ulmea*. Twelve twigs were used, six being sprayed by means of an atomizer with a suspension of spores, while six similar ones were sprayed with sterile distilled

water to serve as checks. Each set was kept under a bell jar, whose inner surface had been lined with moist filter paper, for a period of 42 hours, after which they were left in the normal atmosphere of the greenhouse. A like number of twigs of *U. americana*, whose leaves had unfolded normally outside the greenhouse, were treated in a similar manner. As was to be expected from the failure to secure germination of the ascospores on the leaves of the English elm, no infection occurred on that host. On April 25, however, or after a period of about three weeks, eight leaves of the American elm were found to bear well defined spots quite characteristic of the early stages of *Gnomonia ulmea*. Two of these leaves bore three spots each, another one two, and the other six had only a single one on each. These spots showed well developed pustules of the conidial stage, which is to be described later. In addition to these well defined spots a number of leaves showed small whitish flecks or blotches, thereby indicating that if the experiment had been allowed to continue for a longer period the percentage of infection would have been higher.

Observations on over-wintering

A number of observations have been made on the over-wintering of the fungus on elm leaves under various conditions, and some attempts have been made to hasten its development by placing the leaves under various controlled conditions. Leaves on which the spots occurred were brought into the laboratory, both before and after they had been severely frosted, and some were immersed in water, both at room temperature and in the refrigerator. Others were placed in a moist chamber suspended over water, both in the laboratory and refrigerator, and others were placed in each of these places under their normal conditions of humidity. Still others were suspended over calcium chloride in each of these temperatures in order to assure a dry atmosphere. It was found that no further development occurred in the leaves which were immersed in water, and that the fungus soon died, the perithecia becoming mere empty husks. This was confirmed by comparison with leaves which had wintered normally outside the laboratory. On leaves which had been buried slightly in the soil or were in close

contact with the soil underneath a layer of other leaves, the perithecia were found in early spring to be in approximately the same condition. No further development of the fungus occurred on the leaves either suspended above the calcium chloride or in the normal humidity conditions of the laboratory or of the refrigerator. The fungus in the leaves which had been suspended above water in a moist chamber, however, did continue its development, and by midwinter a few perithecia were found in which the spores were apparently practically mature. In most, and finally in all cases, however, numerous saprophytes developed in such abundance that the *Gnomonia* fungus was overgrown and destroyed before the spores could mature. Other leaves from outdoors were brought into the laboratory at various times throughout the winter and placed in moist chambers, but the same development of extraneous saprophytes soon stopped the observations. In a number of instances observed the *Gnomonia*, apparently in an effort to counteract and overcome the encroachments of the more rapidly developing saprophytic fungi, began to grow vegetatively, and the entire perithecial cavity as well as the ostiolar canal became filled with a mass of interlaced and anastomosed hyphae, so compacted together that under pressure the perithecial wall would break away, but the interior mass would tend to retain its spherical shape. This tissue later died and disintegrated, however, leaving the empty husk of the perithecium. Among the saprophytes which hindered observations a number of forms were invariably present. They were, in the main, *Cephalothecium roseum*, *Phycomyces nitens*, several species of *Penicillium* and *Aspergillus*, an *Alternaria*, a *Pleospora*, a *Crytostyctis*, and a Myxomycete.

Various observations also were made on leaves wintered outside the laboratory. Some leaves were placed on shelves of a wire cage, others were placed on the ground and covered with other leaves and soil, while still others were wrapped in cheesecloth and placed on the surface of the ground. In the leaves placed on the shelves and on the surface of the ground the fungus was found to mature more rapidly than on those leaves covered with other leaves and soil, and a very few perithecia were found on such, which

contained some spores apparently almost mature as early as the middle of February. On only one leaf, however, were any of the perithecia at that time mature enough to expel spores. This leaf was on the shelf of the wire cage, which was placed directly against the south wall of the greenhouse, and was exposed both to the direct rays of the sun and also to the heat rays radiated from the cement wall. In most cases at that time the asci were somewhat more developed than when observed in the fall, but the spores were not yet differentiated. The normal development during the winter, therefore, seemed to be very slow. In leaves which were in especially damp situations, as those buried in the soil or those in intimate contact with the soil under a cover of other leaves, most of the perithecia were found to be dead and disintegrated. In general, it seemed that leaves neither in too exposed nor too moist a situation, as for instance those toward the middle of a pile of leaves, showed the greatest development of the fungus late in winter and early in the spring.

Conidial stage

In every specimen examined in which the ascigerous stage of *Gnomonia ulmea* occurred, I have found constantly associated with it an imperfect or conidial form. This stage was found present from early spring until late fall on every leaf collected, and also on all exsiccati material examined, even the Schweinitzian type specimen previously mentioned. I have examined all available published exsiccati specimens of *Gnomonia ulmea*, as well as more than 100 other specimens obtained for purposes of comparison from various educational institutions and private individuals, including several from the Royal Botanical Gardens, Kew, England, and the herbarium of the University of Geneva, Geneva, Switzerland. The published exsiccati specimens examined are as follows: Ravenel Fung. Amer. Exsic. no. 752; Ravenel Fung. Carol., Fasc. II, no. 63; Ellis and Everhart Fung. Col. nos. 239, 2928, and 3422; Seymour and Earle Econ. Fung. nos. 155a and 155b; Ellis N. Am. Fung. no. 1347; Brenckle Fung. Dakotensis no. 329; Rabenhorst-Winter Fung. Eur. nos. 3661a and 3661b; and von Thümen Myc. Univ. no. 1155.

The conidial layer develops on the stroma which is found on the upper surface of the leaf above the base of the young perithecium (fig. 14). It may cover only a portion of the stroma, and there may be two or even more of them on a single one of the stromata. Again, a stroma may develop, to all appearances identical with those formed above the bases of the young perithecia, but the perithecium be lacking. In this case the conidial pustule invariably covers the entire surface of the stroma. Moreover, in the case of the first pustules formed in the spring, there is usually little or no stromatic base present.

The conidial pustules are quite irregular in outline (fig. 18), although usually approaching a somewhat circular shape. Unless two or more of them coalesce, which frequently, in fact usually, happens, they may become considerably elongated and variously lobed. The size also varies to a considerable extent, due to the coalescing of a number of different pustules. The average size is about 0.5 mm. in diameter, although they may be considerably smaller, and have been seen as large as 0.8 mm. The upper layers of cells of the subcuticular stroma elongate in a direction at right angles to the surface of the leaf and form the conidiophores. These press closely against the cuticle and lift it up somewhat in the course of their development. At the same time they give off a brown coloring matter which is deposited on the inner or lower side of the cuticle, which itself remains colorless. This coloring substance is deposited more deeply at the points between the conidiophores than directly above them, so that the darkened cuticle presents a somewhat reticulate or netted marking, and on casual observation appears to be composed of fungal tissue. This gives the impression that the conidial pustule is of the nature of a dimidiate pycnidium. Closer observation, however, shows that no fungal hyphae enter into this covering layer, and the structure consequently is found to be melanconiaceous in character. The deposition of coloring matter on the cuticular coverings of such acervuli has been noted by KLEBAHN in connection with the conidial stages of *Gnomonia padicola* (**23**), *G. leptostroma* (**22**), and *Gnomoniella tubiformis* (**24**). As previously stated, the same substance is deposited between the cells of the hyphae which make up the

stroma, and which now have become the cells of the hymenial layer from which the conidiophores arise. It is also frequently found deposited between the cells of the epidermis immediately beneath the stroma.

These epidermal cells are not changed to any considerable extent except for crystalline substances occasionally found deposited in them. The fungal hyphae grow down between them and crowd them apart somewhat, but they do not lose their arrangement as a definite layer. The hyphae of the fungus do not penetrate the cells of the host. The conidiophores are crowded together into a very compact layer, and are 8–12 μ long by 1.5–2.5 μ thick. They are without septa, except for an occasional one near the base, and terminate in a threadlike projection on which the spores are borne. The conidia are elongate-oblong or cylindric, bacillar, pointed at one or both ends, straight or sometimes slightly curved, one-celled, hyaline, and measure 5–6 × 1–1.5 μ (fig. 15) in a dry state, but 8–10 × 2–2.5 μ when freshly collected.

Since there is no fungal covering to the conidial layer, the fungus falls into the family Melanconiaceae, and its other characters indicate beyond a doubt that it is a member of the genus *Gloeosporium*. It seems to be quite characteristic of *Gnomonia* to have a conidial stage which is melanconiaceous in character. *Gnomonia padicola* has as an imperfect stage *Asteroma Padi*, but according to KLEBAHN (**26**) no true pycnidium is formed. *Gloeosporium nervisequum* is connected with *Gnomonia veneta*, *Marssonina Juglandis* with *G. leptostyla*, *Gloeosporium quercinum* with *G. quercina*, *Gloeosporium Caryae* with *G. Caryae*, *Gloeosporium Tiliae* with *G. Tiliae*, and *Leptothyrium alneum* with *Gnomoniella tubiformis*. KLEBAHN (**25**) has shown also in connection with *Leptothyrium alneum* that no true pycnidial covering is formed, and that consequently it is melanconiaceous in structure. SACCARDO (**30**) also remarks concerning this species "(perithecio) subinde tamen spurio et ex epidermide mutata et atrata formato."

The genus *Gnomonia* contains a number of species which form no conidial stage, or at least whose conidial stage has not yet been discovered. In so far, however, as the conidial stages have been established in the genus, it is evident that they conform to a

more or less close resemblance to *Gloeosporium*. The *Leptothyrium* of *Gnomoniella tubiformis* is scarcely to be distinguished from a *Gloeosporium; Asteroma* of *Gnomonia padicola* differs from it only in the production of superficial mycelium; and *Marssonina* of *Gnomonia leptostyla* only in its two-celled conidia.

Among the many fungous diseases occurring on the leaves of the elm, only a few have been found whose causative organisms are located in the Melanconiaceae. Three of these belong to the American flora, namely, *Goryneum tumoricolum* Peck, *Septogloeum profusum* (Ell. and Ev.) Sacc., and *Cylindrosporium ulmicolum* Ell. and Ev. I have not seen ELLIS and EVERHART'S specimen of *Cylindrosporium ulmicolum*, and it may be identical with *Phleospora Ulmi* (Fr.) Wallr., since the two descriptions appear very much alike. *Septogloeum profusum* has been reported as occurring on the leaves of *Ulmus alata* and *U. americana*, although it was originally described on *Corylus americana*. Two species of *Gloeosporium*, or rather one species and a variety of the same, have been described on the elm in Europe. One of these, *Gloeosporium inconspicuum* Cav., was described on *Ulmus americana* in Italy, but has never been reported in this country. It was distributed by BRIOSI and CAVARA in "Funghi parassiti" as no. 350. It causes large ochraceous spots on the upper side of the leaf, and has very small bacteriform spores, only 1–2 μ in length. A variety of this species, *Gloeosporium inconspicuum* Cav. var. *campestris* Dor. (15), has been described on *Ulmus campestris* in Russia. From the description this is quite similar in external appearance to the preceding species, but the spores and conidiophores are considerably larger, the spores measuring 3–6 (sometimes 9) $\times$ 1–2 μ. The fungus described as occurring on *Ulmus americana* and other species of elm in America in connection with *Gnomonia ulmea* does not agree in any particular with any of these, and therefore I propose for it the name *Gloeosporium ulmeum*, with the following formal description.

Gloeosporium ulmeum, sp. nov.—Acervuli somewhat gregarious, often confluent, borne on black stromata, usually over the base of the developing perithecium of *Gnomonia ulmea*, covered by the darkened cuticle, which later splits and cracks irregularly

and finally breaks away entirely, subrotund or irregular, averaging 500 μ in diameter, but often as large as 800 μ, epiphyllous, very rarely hypophyllous; conidiophores cylindrical, crowded, occasionally with a septum near the base, 8–12 × 1.5–2 μ, terminating in a threadlike projection on which the spores are borne; conidia elongate-oblong or cylindric, bacillar, pointed at one or both ends, straight or very slightly curved, hyaline, one-celled, 5–6 × 1–1.5 μ in a dry condition or 8–10 × 2–2.5 μ when freshly collected, and extruded in small white masses.

Habitat on the living leaves of *Ulmus americana*, *U. fulva*, *U. alata*, *U. racemosa*, and *U. crassifolia*. Common. Conidial stage of *Gnomonia ulmea* (Schw.) Thüm. and constantly associated with it, the two stages occurring concurrently on the same leaf and spot. Type specimen on *U. americana*, collected at Urbana, Illinois, August 1919, and deposited in the herbarium of the University of Illinois. Differs from *Gloeosporium inconspicuum* Cav. in the very different appearance of the spots and in the larger size of its spores, and from *Gloeosporium inconspicuum* Cav. var. *campestris* Dor. in the character of the spots.

Inoculations with conidia

On April 25 a number of leaves of the American elm were placed in a moist chamber lined with filter paper, and at a definite point on each was placed a drop of distilled water containing a considerable number of spores of *Gloeosporium ulmeum*, the conidial stage of *Gnomonia ulmea*. On June 2 most of these spots were lighter in color than the remainder of the leaf, and on June 5 a few of them showed distinct conidial pustules entirely characteristic of the fungus with which the leaf had been inoculated. On the same day on which this experiment was started a number of leaves of a seedling elm, quite healthy in appearance and growing naturally in the open, were sprayed with a suspension of the same spores in distilled water by means of an atomizer, and the entire twig was inserted into an Ehrlenmeyer flask. The mouth of the flask was closed by means of a split cork in which a channel had been hollowed to fit about the twig. The flask was supported by means of props in such a manner that the twig remained in its proper position. On June 5 the entire new growth of the twig was found to be covered with a practically continuous layer of pustules of *Gloeosporium ulmeum*, all of which were extruding

spores copiously. Not only were the leaves badly infected, but also the petioles and the stem itself.

These experiments, together with the production of the conidial stage on the leaves of the American elm inoculated with the ascospores of *Gnomonia ulmea*, prove conclusively that the two forms are merely stages of the same fungus. The enormous number of spores produced by the conidial stage, as well as the fact that infection secured from inoculations with such spores was much more pronounced and occurred in a somewhat shorter period of time than from inoculation with ascospores, would seem to indicate that the *Gloeosporium* stage is the chief agency through which widespread dissemination occurs in the spring and early summer.

Another Gloeosporium on elm

While working with this fungus, a single tree in a nursery at Oconomowoc, Wisconsin, was found on which the leaf spots were quite different in external appearance from those on the surrounding trees, most of which were abundantly spotted with the *Gnomonia* disease, although the trees were of the same species and had apparently been planted at the same time. Fig. 9 shows a leaf from this collection. The leaf spot is raised considerably more than is the case in the preceding species, giving the portion of the leaf on which it occurs a crumpled appearance where the spot becomes large, and is confined quite closely to the leaf veins, along which it spreads, often extending the entire distance from the midrib to the edge of the leaf, thus forming elongated streaks. The leaf veins also become browned for some distance beyond the spots, although the remainder of the leaf is a normal green. The spots present a gray salt-and-pepper aspect, due to the whitened epidermis over which the black conidial pustules are thickly scattered. The whitened appearance is due also to the disappearance of the contents of the epidermal cells and from the cells of the palisade layer immediately beneath them. This disappearance of cell contents is much more pronounced than in the *Gnomonia ulmea* spot.

The acervuli are very numerous in a single spot and are quite commonly confluent. They are orbicular to oblong in shape, very irregular in outline, and are covered by the darkened cuticle

which persists for a long time, finally cracking and breaking irregularly to allow the dispersal of the spores. They average 800 μ in diameter. The hymenial layer is pseudoparenchymatous, composed of practically colorless cells which are almost isodiametrical in shape. This layer may be even thicker than that described for *Gloeosporium ulmeum*, although it presents an entirely different appearance, and on account of the absence of color does not at all suggest a stromatic base. The layer appears even thicker than it really is on account of the absence of all color from the epidermal cells, which have become entirely filled with small colorless crystals. This is true to a less extent of the adjacent layers of palisade tissue. The conidiophores are closely packed together, and are quite similar to those of *Gloeosporium ulmeum* except for their larger measurements, being 10–15×2–3 μ. They are not as darkly colored as are those of the preceding species, although they are not entirely hyaline. The apex is rather blunt, and the conidiophore terminates rather abruptly in a sterigma-like projection on which the spore is borne. Occasionally two of these sterigma-like processes occur on a single conidiophore. The conidia are much larger, especially in width, and vary considerably in form, from oblong-cylindric to ovate, elliptical, and even pyriform. They measure 8–10×3–3.5 μ (fig. 17), are one-celled, rounded at both ends, straight, and hyaline. In no case was the perithecium of *Gnomonia* or any similar fungus found associated with this spot. I consider it entirely distinct from the conidial stage of *Gnomonia ulmea*, and propose for the fungus the following name and description.

Gloeosporium ulmicolum, sp. nov.—Spots epiphyllous, raised, gray on account of the black acervuli thickly scattered over the whitened epidermal cells, elongated, following the leaf veins, often extending the entire length of the secondary veins which have become browned far beyond the limits of the spot; acervuli epiphyllous, gregarious, subcutaneous, covered by the persistent darkened cuticle which finally ruptures irregularly to allow the dispersal of the spores, averaging 800 μ in diameter, irregular in outline but usually elongated suborbicular; conidiophores in a closely packed layer, dilute-brown, cylindrical, usually nonseptate

but occasionally with a septum near the base, seated on a pseudoparenchymatous hymenial base which is colorless, 10–15×2–3 μ, terminating rather abruptly at the apex in a sterigma-like projection on which the spores are borne; conidia hyaline, one-celled, straight, rounded at both ends, oblong-cylindrical, ovate, elliptical, or even pyriform, 8–10×3–3.5 μ.

Habitat on living leaves of *Ulmus americana*. Oconomowoc, Wisconsin, August 22, 1919. Type specimen deposited in the herbarium of the University of Illinois. This species differs from *Gloeosporium ulmeum* in the shape and appearance of the spots, in the fact that it is not associated with a perithecial stage as that fungus constantly is, in the absence of a black basal stroma, and in the larger spores. In external appearance the two forms are quite distinct. It differs also from *Gloeosporium inconspicuum* Cav. and *G. inconspicuum* Cav. var. *campestris* Dor. in the character and appearance of the spot and in the much larger spores.

Principal European leaf spot

SYSTREMMA ULMI (Schleich.) Thiess. and Syd.—The leaf spot of the elm occurring in Europe on *Ulmus campestris*, *U. effusa*, and *U. glabra* has a somewhat superficial resemblance to that produced in this country by *Gnomonia ulmea* (Schw.) Thüm. This may readily be seen by comparing fig. 6, which shows the European spot on a leaf of *Ulmus campestris*, with figs. 4 and 5, which are leaves of *U. americana* affected by the *Gnomonia*. The two diseases have been much confused in this country, and it has been quite common for American plant pathologists and mycologists to speak of the latter fungus under the name of the European organism. In examining specimens of the *Gnomonia* spot in various collections in this country, I have found it quite as often referred to in this manner as under its true name or synonyms. There are two references in literature to the occurrence of the disease caused by *Systremma Ulmi* in America, in addition to various others which are clearly due to a confusion of the two forms. One of these cases is in the report by TRELEASE (**40**) of the presence in Wisconsin of *Phyllachora Ulmi* Fuck., which name is a synonym of *Systremma Ulmi*. On examination of the specimen, which is in the museum of the Shaw Botanical Gardens at St. Louis, Missouri, it was found that the disease was the American form, caused by

Gnomonia ulmea. TRELEASE also reported the presence on the same leaf of *Septoria Ulmi* Fr., a synonym of *Phleospora Ulmi* (Fr.) Wallr., which at that time was thought to be the conidial stage of *Phyllachora Ulmi*, but I was unable to find any trace of it on the specimen examined. In material sent from the University of Geneva, Switzerland, I found another specimen, evidently from this same collection by TRELEASE and labeled in the same manner. It also was *Gnomonia ulmea*.

The second reference to the occurrence of *Systremma Ulmi* in this country is by ELLIS and EVERHART (**16**), who stated that a specimen of *Dothidella Ulmi* (Duv.) Wint., which name is merely another of the numerous synonyms under which the European organism is known, was sent to SCHWEINITZ by TORREY from New York. They added that they could not find any other references to this species being found in this country, and that they have seen no American specimens. I find in SACCARDO'S (**33**) *Sylloge Fungorum* in the description of *Sphaeria apertiuscula* Schw. on *Ulmus fulva*, collected by TORREY in New York, the statement added that the upper side of the leaf is covered with *Dothidea Ulmi*. This is evidently the specimen to which ELLIS and EVERHART were referring, as both the names used are synonyms of *Systremma Ulmi*. I have not seen this specimen, and there is a possibility that it is really a specimen of the European leaf spot, but it is hardly likely, especially since it has never been collected in this country since, nor has it ever been reported as occurring on *Ulmus fulva* at any other time, either previous to that collection or later.

I found in specimens sent from the Royal Botanical Gardens at Kew, England, among those labeled as belonging to the herbarium of BERKELEY, three specimens purporting to have been collected by DRUMMOND in arctic America. These were undoubtedly specimens of *Systremma Ulmi*, and, although the host was not named, the leaves possessed the somewhat three-lobed character peculiar to the Scotch elm, *U. glabra*. This is not native to America, and one would hardly expect to encounter an introduced species in the arctic regions. For these reasons I believe that these three specimens represent some European collection

which has in some manner accidentally become mixed with DRUMMOND'S arctic collections while they were in the process of being mounted at the museum. This seems all the more probable when it is noted that the handwriting on the labels is the same as that on a great many of the other specimens from the same museum. It would seem, therefore, quite probable that *Systremma Ulmi* does not occur at all in America. Although ELLIS and EVERHART place the causative organisms of the two diseases in the same genus, they express a caution against confusing the two, stating that although they have spores essentially the same they differ very markedly in other characteristics. In spite of the fact that the external appearances of the two spots seem quite similar to the casual observer, as soon as one sections them the very marked differences between the two fungi become apparent. Fig. 10 represents a section through the stroma of *Systremma Ulmi*. It will be seen that the black stroma, to which the external resemblance between the two forms is due, is in this case subepidermal, while in *Gnomonia ulmea* it is subcuticular only. In the *Systremma* the asci are produced in locules without true perithecial walls, which are imbedded in the stroma and open on the upper side of the leaf, while in *Gnomonia* the perithecia, truly sphaeriaceous in character, are located in the leaf tissue beneath the stroma and open on the under side of the leaf. *Gnomonia ulmea*, therefore, belongs to the Sphaeriales, while *Systremma Ulmi* belongs to an entirely different order, the Dothidiales. Although the asci and spores of the two differ but little in form, both are slightly larger in *Systremma* than in *Gnomonia*.

I have examined all available published exsiccati specimens of this fungus, as well as about 200 other specimens borrowed for purposes of examination and comparison from the Royal Botanical Gardens at Kew, and from the University of Geneva, and from a number of institutions and individuals in this country. The published exsiccati of this fungus examined were as follows: BERKELEY Brit. Fung. no. 192; VIZE Mic.-Fung. Brit. no. 277; COOKE Fung. Brit., Ser. I, no. 184; BRIOSI and CAVARA Fung. paras. no. 73; POLLACCI Fung. Longobardiae Exsic. no. 287; SACCARDO Myc. Ven. nos. 231 and 642; ROUMEGERE Fung. Sel. Exsic. nos. 466 and

5761; Fl. Gall. et Germ. Exsic. no. 1000; SCHLEICHER Crypt. Exsic. no. 73; HOLL, SCHMIDT, und KUNZE Deut. Schwamme no. 32; DESMAZIERES Crypt. Fr., Ser. I, no. 284; MONGIER et NESTLER Stirpes Crypt. no. 766; VON THÜMEN Fung. Austr. no. 499; VON THÜMEN Myc. Univ. no. 2064; FUCKEL Fung. Rhen. nos. 1013 and 2265; SYDOW Myc. Mart. no. 256; LUNDH. Fung. Hung. no. 374; RABENHORST Herb. Myc. no. 658; WESTEND. Herb. Crypt. no. 111; KRUEGER Fung. Sax. no. 1514; ERIKSSON F. Scand. nos. 292a and 292b.

The synonymy of the fungus is as follows: *Systremma Ulmi* (Schleich.) Thiess. and Syd., Die Dothidiales, Ann. Myc. **13**:334. 1915; *Sphaeria Ulmi* Schleich., Crypt. Exsic. no. 73, sec. de Candolle Fl. Franc. **2**:288. 1805; *Sphaeria xylomoides* DC., Fl. Franc. **2**:288. 1805; *Sphaeria Ulmi* Duv., Hoppe's Bot. Taschenb., 105. 1809; *Xyloma sticticum* Mart., Crypt. Flor Erlang., 309. 1817; *Sphaeria ulmaria* Sow., Eng. Fung., *pl. 374. fig. 3; Polystigma Ulmi* Link, Rab. Handb. **1**:167; *Dothidea Ulmi* Fr., Syst. **2**:555. 1823; *Phyllachora Ulmi* Fuck., Symb. 218; Sacc. Syll. Fung. **2**:594. 1883; *Euryachora Ulmi* Schroeter, Crypt. Fl. Schles. 3^2:473.

The conidial stage of this fungus is *Piggotia astroidea* B. and Br.

Other leaf spots of elm

IN AMERICA

MYCOSPHAERELLA ULMI Kleb. (**28**).—This is the ascigerous stage of *Phleospora Ulmi* (Fr.) Wallr., which has been reported both in America and Europe as the cause of a leaf spot on *Ulmus campestris*, *U. glabra*, and *U. americana*. In the conidial stage it is said sometimes to do considerable damage to nursery stock and young trees. STEWART (**36**) states that it has been observed several times to cause extensive defoliation of young elms in New York. Numerous, small, reddish-brown spots appear on the upper side of the leaves, which in consequence gradually turn yellow, the margin becomes brown and rolls up, and they fall early in the season. The spores ooze out in minute cirrhi which dry on the lower side of the leaf surface and form small whitish patches. SACCARDO (**31**) states that on account of the absence of pycnidia it leans toward *Septogloeum*, and it is sometimes known by that

name. CLINTON (9) and BRIOSI and CAVARA (5) also maintain that it belongs to that genus and call it *Septogloeum Ulmi* (Fr.) Bri. and Cav. CLINTON also suggests that *Cylindrosporium ulmicolum* Ell. and Ev. is possibly not distinct from this species. I have not seen the ELLIS and EVERHART specimen, and admittedly the two descriptions are very similar, especially when one takes into consideration the very great differences in spore measurements recorded by various collectors of *Phleospora Ulmi*. STEWART records as follows: "As we have found them, they (the spores) are 3- or 4-septate, usually quite strongly curved, and measure 34–38×5.5–6.5 μ. In no. 157 of *Seymour* and *Earle's* Economic Fungi, on *Ulmus fulva*, the spores are 3-septate, straight, and measure 33.5×6.3 μ. In no. 648 of *Krieger's* Fungi Saxonici, on *Ulmus campestris*, they are 3- or 4-septate, strongly curved, and measure 49.5×4.7 μ." Under the name of *Septoria Ulmi* Fr., this fungus was regarded by FUCKEL as the spermagonial stage of *Phyllachora Ulmi*, a synonym of *Systremma Ulmi*, but it was shown by KLEBAHN (23) that it had no connection with that fungus, but was the conidial stage of *Mycosphaerella Ulmi*, which develops on the dead leaves in the spring.

CYLINDROSPORIUM ULMICOLUM Ell. and Ev.—Spots becoming flavous; acervuli minute, hypophyllous; conidia cylindraceous, 45–65×4 μ, hyaline, multinucleate, coming out in minute white caespitules. Reported on leaves of *Ulmus alata* in Mississippi. In spite of the differences in spore measurements, the possibility has been suggested that this is not different from *Phleospora Ulmi*.

SEPTOGLOEUM PROFUSUM (Ell. and Ev.) Sacc.—Spots epiphyllous, flavous; acervuli scattered, hypophyllous, large; conidia coming out in white cirrhi, cylindrical, oblong, granular, 3-septate, 25–30×6–7 μ. Reported on living leaves of *Ulmus americana* and *U. alata*, although it was first described on *Corylus americana*.

CERATOPHORUM ULMICOLUM Ell. and Hark.—Causes small, suborbicular, dirty-brown, amphigenous spots with a white center, 0.5–1 cm. in diameter, on living leaves of *Ulmus fulva*. Noted from several places in the United States.

PHYLLOSTICTA ULMICOLA Sacc.—Reported as being present in Wisconsin by DAVIS (13) who states as follows:

Under this name I am recording the occurrence of a fungus having the following characteristics: Spots indefinite, immarginate, orbicular, light-brown, becoming cinereous above and lacerate, finally falling away in fragments, 3–7 mm. in diameter, sometimes confluent; pycnidia epiphyllous, scattered, black, globose to depressed, 60–80 μ; sporules globose to elliptical, olivaceous-hyaline, continuous, 3–6$\times$2–3 μ. On *Ulmus americana*, Tisch Mills, August 3, 1917. *Ulmus racemosa*, August 5, 1917. This is probably a member of a group of forms of which various names have been applied in Europe and America.

It has also been reported from a number of other states, among them Michigan, where it is said to occur on *Ulmus fulva*.

PHYLLOSTICTA CONFERTISSIMA Ell. and Ev.—Spots red-black, amphigenous; pycnidia 75 μ in diameter; spores allantoid, hyaline, 3–4$\times$1 μ. On leaves of *Ulmus fulva* in Kansas.

PHOMA CINCTA B. and C.—Spots irregular, depressed, with a white border; spores oblong, narrow, 6–8 μ long. Reported on leaves of *Ulmus americana* in South Carolina.

EXCIPULA ULMICOLA Schw.—Causes widely expanded indeterminate spots on the upper side of the leaf, becoming somewhat spotted with gray on both sides, with a broad, fuscous margin; pycnidia copious, immersed, excipuloid, punctiform, black, depressed in center and becoming gray. Reported as somewhat rare on cast-off leaves of *Ulmus fulva* about Bethlehem, Pennsylvania.

CORYNEUM TUMORICOLUM Peck.—Forming scattered, suborbicular, pale spots, bounded by a red-brown border on living leaves of *Ulmus americana* in the Adirondack Mountains.

SPHAERIA APERTIUSCULA Schw.—Scattered, fuscous-black, minute, arising from the swollen parenchyma; at first innate, at length opening by a very wide mouth, but evacuate within; resembles a small *Peziza*. Recorded as occurring on the lower side of leaves of *Ulmus fulva* in New York.

RHYTISMA ULMI Fr.—Minute, difformous, gyrose with an elevated margin, at length dehiscing labiately. Reported on leaves of *Ulmus* in North America.

MELASMIA ULMICOLA B. and C.—Spots reddish, indefinite; pycnidia punctiform; spores minute, oblong-botuliform. COOK (10) speaks of it as the *Melasmia* stage of *Rhytisma Ulmi*, and reports it as very common in New Jersey.

List of species occurring in Europe only

Acremoniella pallida Cooke and Mass., *Actinonema Ulmi* Alleschr., *Ascochyta ulmella* Sacc., *Asteroma angulatum* Desm., *A. Fuckelii* Sacc., *Cladosporium hypophyllum* Fuck., *Exoascus campester* Sacc., *Gloeosporium inconspicuum* Cav., *G. inconspicuum* Cav. var. *campestris* Dor., *Laestadia comedens* (Pass.) Sacc., *Pestalozzia maculicola* Rostr., *Phyllosticta bellunensis* Mart., *P. lacerans* Pass., *P. ulmaria* Pass., *P. Ulmi* West., *Sphaerella Oedema* (Fr.) Fuck., *S. insularis* Wallr., *Sphaeria ulmifolia* Pass., *Sporodesmium Ulmi* Fuck., *Stagonospora ulmifolia* (Pass.) Sacc., *Stigmella Castagneana* (Mont.) Sacc., and *Taphrina Ulmi* Johans.

Fossil leaf spots of elm

In Meschinelli's *Fungorum Fossilium Iconographia* seven species are given occurring on leaves of fossil elms. Plates and figures are included for six of these, but they are very unsatisfactory in most cases, and in some instances one cannot be at all sure that the spot is even of fungal origin. The species are as follows: *Sphaerites perforans* Goepp., *S. glomeratus* (Engelh.) Mesch., *S. rhytismoides* (Ettingsh.) Mesch., *Rhytismites ulmicola* (Ettingsh.) Mesch., *R. Ulmi* (Ludw.) Mesch., *Depazites Ulmi* (Ettingsh.) Mesch., and *Xylomites* sp. (Boulay) Mesch.

Summary

1. *Gnomonia ulmea* (Schw.) Thüm., the cause of the most common elm leaf spot in America, has been reported as occurring on five of the six native species of elm in this country and is of wide distribution, being found throughout the entire range of its hosts. Its normal host, on which it is most commonly found, is *Ulmus americana*. The fungus is not ordinarily of much economic importance, but may cause considerable injury to seedlings and young trees in nurseries by producing premature defoliation.

2. Unlike most of the Ascomycetes, the perithecial stage of the fungus begins its development in the living leaf early in the spring. The young perithecium develops in the palisade tissue beneath a subcuticular black stroma.

3. An ascogonium is found in the young perithecium, but there is no trichogyne.

4. An interascicular pseudoparenchyma is found present in the perithecium almost until the period of maturity.

5. In the process of ascospore expulsion an entire ascus enters the lower part of the ostiolar canal, and the eight spores are apparently discharged simultaneously.

6. The ascospores could not be made to germinate either in tap or distilled water, in nutrient solutions, on solid media, or on the living leaves of the English or Scotch elm. They germinated readily on the leaves of the American elm, however, thus indicating that they require a special stimulus of some sort which is present in the leaves of some species of *Ulmus*, but absent in others.

7. The fungus matures most rapidly during the winter on leaves which are neither too exposed nor in too damp a situation. When immersed in water or in intimate contact with the soil, the fungus dies, and only the empty husks of the perithecia remain.

8. A conidial stage was found constantly associated with this ascigerous form. It is described as a new species, *Gloeosporium ulmeum*.

9. The connection between the two forms was conclusively proven by inoculations. The ascospores of *Gnomonia ulmea* gave rise to spots on the leaves of *Ulmus americana* which were entirely typical of *Gnomonia*, and which bore the acervuli of *Gloeosporium ulmeum*. The spores of this form also readily infected the leaves of the American elm, and appeared even more virulent than were the ascospores, indicating that this form is probably the agent by which extensive dissemination of the fungus is assured in spring and early summer.

10. A new leaf spot of the American elm, caused by *Cloeosporium ulmicolum*, another new species, is described. This species differs from the one previously described in the characters of the spot and in the larger size of the spores.

11. *Systremma Ulmi* (Schleich.) Thiess. and Syd. causes a leaf spot of the European elms in Europe. *Gnomonia ulmea* has been very much confused with this fungus, and as a consequence has gotten into the literature as occurring in this country. The probability is, however, that it does not occur in America at all.

It is a member of the Dothidiales, while *Gnomonia ulmea* belongs to the Sphaeriales.

12. Other species of fungi producing leaf spots on the elm are listed with a brief comment on each of the American forms.

13. Seven species of fungi are listed on the leaves of fossil elms.

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EXPLANATION OF PLATES VIII–X

PLATE VIII

FIG. 1.—Two perithecia of *Gnomonia ulmea* in almost mature condition, showing interascicular pseudoparenchyma, and also elongated beaks and periphyses-lined ostiolar canal.

FIG. 2.—Early stage in development of perithecium of *Gnomonia ulmea*, showing position in palisade layer; subcuticular stroma above has given rise to acervulus of imperfect form of fungus, *Gloeosporium ulmeum*.

FIG. 3.—Elm leaf, showing one type of *Gnomonia* spot; note absence of border of dead or browned tissue and that stromata tend to coalesce.

FIG. 4.—Elm leaf, showing another type of spot; black stromata surrounded by border of light brown dead tissue.

FIG. 5.—Same as fig. 4 except that epidermis covering stromata has begun to wear away, giving spot a lighter, somewhat ashen, appearance.

PLATE IX

FIG. 6.—Leaf of English elm, showing leaf spot caused by *Systremma Ulmi;* note that each spot is but a single stroma, much more definite in outline than that caused by coalesced stromata of *Gnomonia ulmea*, and that they are raised much more above surface of leaf; note also wrinkled or papillate appearance of stroma.

FIG. 7.—Schweinitzian type specimen of *Gnomonia ulmea.*

FIG. 8.—Perithecium of *Gnomonia ulmea* at earliest stage in development of beak and ostiole; dark portion of perithecium represents young asci just beginning development; note psuedoparenchymatous contents of perithecium.

FIG. 9.—Elm leaf, showing spots caused by *Gloeosporium ulmicolum*, sp. nov.; note manner in which spots follow the veins; compare with figs. 3, 4, 5, 7, and 12 for differences from spot caused by *Gnomonia ulmea.*

FIG. 10.—Section through stroma of *Systremma Ulmi*, subepidermal in origin; note absence of perithecial walls, and that asci are borne in locules in stroma which open on upper side of leaf.

FIG. 11.—Single spot, fig. 12*a*, enlarged 10 diameters, showing isolated character of stromata of *Gnomonia ulmea.*

FIG. 12.—Elm leaf, showing stromata of *Gnomonia ulmea* as they sometimes appear, widely separated in spot and somewhat concentrically arranged.

FIG. 13.—Very young stage in development of perithecium of *Gnomonia ulmea*, showing pyriform shape at this stage, and connection with stroma.

PLATE X

FIG. 14.—Acervulus of conidial stage, *Gloeosporium ulmeum*, sp. nov., formed above young perithecium of ascigerous stage, *Gnomonia ulmea.*

FIG. 15.—Spores of *Gloeosporium ulmeum.*

FIG. 16.—Very young stage in development of *Gnomonia ulmea: a*, sheathing hypha; *b*, ascogonium; *c*, "suspensor" or "infection thread"; *d*, vegetative hyphae which break through stroma to outer surface.

FIG. 17.—Spores of *Gloeosporium ulmicolum.*

FIG. 18.—Single acervulus of *Gloeosporium* stage of *Gnomonia ulmea*, showing manner of cracking to allow dispersal of spores; hyphae about acervulus are those of basal stroma as viewed from above.

FIG. 19.—Ascus and ascospores of *Gnomonia ulmea.*

FIG. 20.—Germinating spores of *Gnomonia ulmea.*